CHAPTER

17

Paleotemperature Estimates for the Lowland Americas Between 30°S and 30°N at the Last Glacial Maximum

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Abstract

Paleoecological data for the lowland neotropics and subtropics between 30°N and 30°S are compiled to provide an overview of climatic conditions at the time of the last glacial maximum. A clear consensus emerges from both fossil pollen and noble gas proxies that lowland climates were ca 5°C cooler at 18,000 ^{14}C B.P. than they are now. In many records, this period appears to have been the coldest portion of the last glacial episode, but in others, periods between 33,000 and 30,000 ^{14}C B.P. and between 14,000 and 12,000 ^{14}C B.P. appear to have been somewhat cooler. These data suggest that while there was a general cooling across the lowlands, local climates were subject to periodic warmer and cooler events. More data are needed to determine the effects of such climatic oscillations on biotic assemblages in the lowland neotropics and subtropics.

Within the community of paleoclimatologists, considerable debate continues regarding the amount of precipitation reduction at the last glacial maximum. Some drying is probable, but more data and improved methods to quantify paleoprecipitation are needed to resolve the current debate.

Resumen

Los datos paleoclimáticos de las zonas bajas neotropicales entre los 30°N y 30°S han sido recogidos para proporcionar una sinopsis de las condiciones climáticas en tiempos del último máximo glacial. Un evidente consenso aparece, con datos de polen fósil y de gases nobles, respecto a que estos climas tenían 5°C menos en 18.000 ^{14}C B.P. que en la actualidad. En muchos registros, este periodo parece haber sido el momento más frío del último episodio glacial, pero en otros, los periodos entre 33.000 y 30.000 ^{14}C B.P., y entre 14.000 y 12.000 ^{14}C B.P. parecen haber sido algo más fríos. Estos datos sugieren que mientras tenía lugar un enfriamiento general en las zonas de estudio, los climas locales estuvieron sujetos a periódicos eventos cálidos y fríos. Serán necesarios más datos para determinar los efectos de las oscilaciones climáticas en los conjuntos bióticos en la zona tropical y subtropical.

En el seno de la comunidad de paleoclimatólogos, continua el debate con respecto a la reducción de la cantidad de precipitación en el último máximo glacial. Es probable alguna sequía, pero más datos y la mejora de los métodos para cuantificar la paleoprecipitación son necesarios para resolver el actual debate.

17.1. INTRODUCTION

An accurate representation of the temperature gradients from the poles to the equator is fundamental to deriving reliable climate models. A persistent problem for modelers is to establish appropriate temperature gradients for the past. It is probably fair to say that both research effort and confidence in paleotemperature reconstructions are positively correlated with increasing latitude. Robust temperature reconstructions for the last 18,000 years at high latitudes are based on core records from deep ocean sediment, ice caps, and lake sediments. In the midlatitudes of the Americas (30°–70°N), an abundance of marine oxygen isotope and foraminiferal records provide data on past sea surface temperature (SST) (e.g., Broecker, 1986; CLIMAP Project Members, 1976, 1981). Terrestrial and nearshore sedimentary records have drawn on a wide array of proxy indicators that provide paleotemperature records for the land (e.g., Davis, 1981; Webb, 1987; Heusser, 1995; Haberle, 1998; Smith and Betancourt, 1998). On the whole, the temperature reconstructions of midlatitude terrestrial and oceanic systems are in close agreement (e.g., CLIMAP Project Members, 1981; Kutzbach and Guetter, 1986). In South America, at equivalent latitudes, a growing body of palynological, glaciological, and entomological data provide convincing paleotemperature reconstructions from the present to 18,000 ^{14}C B.P. (e.g., Markgraf, 1993). However, comparatively few records from nearshore or terrestrial environments are available for the subtropics to the equator (30°–0°) in either hemisphere.

Paleoclimate data for tropical regions began to appear in the 1960s with fossil pollen records from montane Colombia (van der Hammen and Gonzalez, 1960) and Costa Rica (Martin, 1964). Mercer began investigations of relict moraines in Peru (e.g., Mercer and Palacios, 1977) and spawned an active field of Andean moraine-based reconstructions of high-elevation cooling (e.g., Clapperton, 1987; Seltzer, 1990). In the 1980s, further data were gathered from the Sabana de Bogotá and other sites in Andean Colombia (Hooghiemstra, 1984, 1989) and the Junín Plateau of Peru (Hansen et al., 1984). By the mid-1980s, a consensus emerged of high-elevation cooling during glacial times. Some glaciological data from Ecuador suggested that mid-Pleistocene (ca. 40,000–30,000 ^{14}C B.P.) ice advances had pushed further downslope than those of 18,000 ^{14}C B.P. (Clapperton, 1987). However, it was not clear whether these lowermost moraines were the product of lower temperatures or greater moisture availability. Van der Hammen and Hooghiemstra (2000) suggest a cooling of ca. 8°C in the Andes at 18,000 ^{14}C B.P. and suggest that this was the coolest period documented in the late Pleistocene at the Sabana de Bogotá.

The CLIMAP (1976) SST estimates coincided with conventional biogeographic wisdom (e.g., Haffer, 1969; Vanzolini, 1970), which demanded that lowland tropical temperatures remained constant, or nearly so, during glacial cycles. However, this hypothesis remained untested because of logistic difficulties and technical doubts about the feasibility of lowland tropical palynology (Faegri, 1966). The first data that provided a glimpse of glacial conditions from the lowland neotropics were equivocal.

Van der Hammen and his team pioneered lowland palynology in South America with core sections from Ogle Bridge, Guyana, and the Alliance Borehole, Surinam (van der Hammen, 1963, 1974; Wijmstra, 1969). In both sequences the records show Poaceae-rich pollen spectra replacing mangrove and mesic forest pollen. A reasonable interpretation is that closed forest was replaced by more xeric communities. However, as neither sequence is dated (apart from one date of >45,000 ^{14}C B.P.), it is impossible to assign these spectra to any particular pre-Holocene interval. Similarly, two undated diagrams from Rondônia on the southern fringe of forested Amazonia apparently depict a northward range expansion of savanna elements. Absy and van der Hammen (1976) attributed the savanna expansion to glacial age aridity. Though tantalizing, these data sets did not provide reliable climatic data for the last glacial period. Better evidence for Pleistocene drying came from the Lake Valencia record, Venezuela, which suggests climates were cooler and drier during glacial times than now (Bradbury et al., 1981).

In this chapter, we provide an overview of a growing body of well-dated paleoecological data for the lowland (<1200 m elevation) neotropics and provide a consensus estimate of lowland neotropical paleotemperature at 18,000 ^{14}C B.P.

17.2 METHODS

The principal techniques used to date in reconstructions of terrestrial paleotemperatures for the lowland neotropics have been pollen in lake sediments and noble gases dissolved in groundwater. The collection and processing of pollen samples are broadly standardized around the techniques outlined by Faegri and Iversen (1989). The area of methodology that is worthy of review is in the quantification of paleotemperature.

Lowland palynological temperature reconstructions are generally based on the movement of indicator taxa. Apparently, stenothermic pollen taxa, or ones that at least occupy identifiable habitat ranges, are selected as indicator species. The modern range of these taxa is then compared with past ranges, and from this an inference is made about past climate. Van der Hammen and Gonzalez (1960) were the first researchers to correlate the downslope movement of pollen taxa to changes in temperature. They achieved this translation through the application of moist air adiabatic lapse rates. For instance, if in the past a species was documented 1000 m downslope of its present position, and the local moist air adiabatic lapse rate was 5°C of cooling per 1000 m of ascent, the paleotemperature change was 5°C cooler than present values.

Most researchers have since adopted this method of calculating temperature change, but we should examine some of its assumptions.

The first assumption is that there has been no significant evolutionary change in the requirements of the pollen taxa. Given the short time interval (20–50 tree generations since the last glacial interval), it is unlikely that evolution is a major problem, especially when more than one pollen taxon is exhibiting the same trend.

A second assumption is that the moist air adiabatic lapse rate has not changed. Studies of moist air adiabatic lapse rates reveal that they are rigidly constrained by the physical properties of air and are unlikely to have wavered outside of a narrow range (Webster and Streten, 1978; Rind and Peteet, 1985). Moist air associated with cloud forests and the wet lowland forests has a lapse rate of ca. 5°C. At the other extreme, desert dry air can have lapse rates approaching 7°C (Webster and Streten, 1978). Thus, the greatest potential change would be 2°C / 1000 m of ascent. For many years, changes in ice age lapse rates were used to explain the anomalously warm oceans compared with the cool Andes (e.g., Haffer, 1991). However, as will be demonstrated later, when there is evidence of cooling, the forests are mesic or humid, indicating the presence of moist air. In other words, the *Alnus*, *Hedyosmum*, *Weinmannia*, *Podocarpus*, and *Drimys* populations that spilled down the flank of the Andes were of species adapted to the moist conditions of the cloud forest in which they now live. With paleoecological evidence to show that elevations as low as 1000 m above sea level (asl) had saturated air, it is not possible to discount evidence of cooling on the basis of steepened lapse rates.

A further criticism of using pollen to describe annual average paleotemperature is that the range of plants (therefore the elevation at which they grow) is determined not by mean annual temperatures, but by absolute minima. The distribution of plants is determined by the coldest night they survive rather than mean temperature. One way to test whether observing minimum temperatures rather than mean temperatures would yield more information on species ranges is to plot both mean and minima data against elevation, and fit a regression line for each set of values. If the regression lines have a similar slope, then it is legitimate to use plant ranges to derive mean temperature values. Of course, the minima are likely to be more ecologically revealing in terms of determining the cause of the distribution, but that is a separate issue.

Detailed long-term climatic data on temperature maxima and minima are scarce for the neotropics, but a data set that provides a transect of daily minimum temperatures from Manaus, across lowland Ecuador, to the crest of the Andes is shown in Fig. 1. This data set is far from perfect, and some records were kept for only a few years. A relatively short run of data will not affect the mean temperature values, but may underestimate occasional bouts of extreme cooling. However, the lowland records did include an episode of *friagem* cooling, and it is unlikely that much lower temperatures would be experienced under modern conditions. As a first approximation, this data set clearly makes the point that tropical temperature minima are generally closely correlated to mean temperatures.

Climatic requirements of *Araucaria*—e.g., mean winter temperature, number of days of frost, and length of dry season—are used by Ledru (1991, 1992, 1993) and De Oliveira (1992) to infer paleoclimates associated with a Pleistocene range expansion of this genus. If it is assumed that *Araucaria* distributions are bound by these variables, a comparison of climatic data from the modern range with that of the Pleistocene range pro-

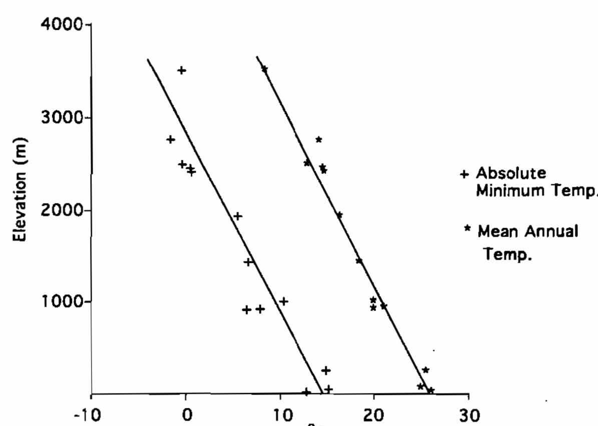

FIGURE 1 Modern mean annual and minimum temperatures for Ecuadorian weather stations (Centro Ecuadoriano de Investigación Geográfica [CEDIG] 1983) plotted against elevation. The regression line through the mean temperature data represents a 5°C / 1000 m ascent, representing moist air adiabatic lapse rate. The line through the minima data represents a best-fit regression line. Note how the two lines for minimum and mean temperatures are virtually parallel.

vides estimates of changes in temperature and precipitation. This technique is freed from assumptions about lapse rates and, therefore, provides a valuable alternate means to measure paleotemperature. The above-cited authors used the movement or expansion of *Araucaria* forest from southern into southeastern Brazil (20°–25°S) to infer past-climate change. Behling and Lichte (1997) adopted a similar technique as they documented the movement, or expansion, of subtropical grassland from southern into southeastern Brazil. They found Pleistocene assemblages rich in subtropical grassland species approximately 7° of latitude farther north than their present range. Basing their climatic inference on modern weather data for the two areas, they infer an ice age cooling of between 4° and 8°C.

Another way to assess temperature using whole community values rather than indicator species has formed the basis of conventional transfer functions (e.g., Imbrie and Kipp, 1971; CLIMAP Project Members, 1976; Bonnefille et al., 1990). A number of problems are inherent in this approach, such as the lack of modern analogs for past assemblages and an inherent tendency toward underestimating any change. Many pollen taxa within an assemblage provide no detailed climatic information and can be regarded as catholic. If a full range of analog sites existed, the diluting effect of many catholic species would not matter, but without a full array of analogs, the presence of catholic species inevitably moderates the signal of climate change. The solution is to exclude the catholic species from the analysis and use a selection of stenothermic species. This compromise between using single indicator species and whole communities can be used to estimate response surfaces for precipitation or temperature. This technique could provide a paleothermometer that is independent of lapse rates.

It has been suggested that biome boundaries could be used to model past-climate change. The strength of the biome approach is that it is independent of lapse rates, it does not rely on modern communities being exactly those of the past (though intermediate vegetation types between recognizable modern biome types are a problem), and it should reduce subjectivity in interpretation. However, this technique also has problems that are particularly severe in the tropical lowlands (Marchant et al., in press).

Biome models assume that there will always be a biome to replace the existing one, but in the case of the lowland tropics there is none. Applying such models to lowland tropical paleoecology brings into focus a philosophical problem inherent in the concept of the biome—that modern conditions are normal. But, they are not. Glacial age conditions were the norm of the last 2 million years, and modern times are oppressively hot. At 0° latitude and at 50 m elevation in the middle of the vast Amazonian plain, there is nowhere to retreat when it gets warmer. Some of the most stenothermic species that flanked the Andes escaped upslope to cooler climates at the beginning of the Holocene and will stay there until normal conditions return. The majority of species stay where they are because there are no *hotter adapted* species to displace them. Thus, the lowland tropics are unique—they really cannot show a warmer than usual signal (remember glacial conditions are the norm), other than an upslope migration of a few species. Biome models may be more appropriate in other settings, but they will fail in the lowland tropics because the lowland tropic biome is an endpoint in the biome continuum.

A second problem with taking the results of biome models at face value is more mechanical. Because the models treat a biome as a uniform climatic mass, the only changes indicated are when one biome replaces another. In other words, two regions that occur within the same biome—say, Atlanta and New York, which both occur in a temperate forest biome—would be accorded the same climate. It is clear that there could be substantial climatic change and yet no change in biome. Where biomes do change, relatively massive changes in climate are inferred. Neighboring areas that experience similar climatic change, but are judged to be biome constant, are suggested to have had a constant climate. Not all climate effects are geographically gradual, but we suggest the biome is too coarse a descriptive unit to elucidate paleoclimatic change in the tropics.

The only possible biome change that could be registered in Amazonia would be a transition from forest to savanna. Clearly, it is unsatisfactory to reduce all possible climatic variants to a simple "either savanna or forest." Under this kind of biome construction, vast areas will show no climatic change, and within the constructs of their model they are precisely correct. During the last glacial period, savanna did not replace large areas of forest, nor did lowland forests give way to Paramo grasslands or even to montane forest. Given the observed vegetation changes documented in the Amazon basin, over the greatest portion of the area there were no changes in biome; but this does not mean that there was not a significant change in temperature or precipitation.

17.3. NOBLE GASES DISSOLVED IN GROUNDWATER

In recent years, a new approach that provides an independent paleotemperature proxy has evolved, i.e., the measurement of atmospheric noble gases dissolved in radiocarbon-dated groundwater. The principle of the "noble gas thermometer" is based on the temperature dependency of the solubility of noble gases (Ne, Ar, Kr, and Xe, and in certain cases also N_2) in water (Mazor, 1972; Andrews and Lee, 1979; Stute and Schlosser, 1993). Groundwater percolating through the unsaturated zone continually equilibrates with soil air until it reaches the water table. While moving deeper into the subsurface, the groundwater becomes isolated from the atmosphere and carries the imprinted climate signal, recorded by its noble gas composition, along. Fluctuations of the water table typically result in the partial or complete dissolution of trapped air bubbles. In most cases, the individual processes can be separated by an iterative procedure (Stute and Schlosser, 1993; Stute et al., 1995). In suitable groundwater flow systems, the resulting *noble gas temperature* closely reflects the mean annual ground (soil) temperature at the water table in the recharge area. This climate signal is best preserved in confined aquifers. However, a groundwater flow system acts as a low-pass filter (Stute and Schlosser, 1993). At 18,000 ^{14}C B.P., for example, this smoothing effect is equivalent to a moving average of several thousand years. The weaknesses of this technique are the uncertainty in the excess air correction, the radiocarbon dating, and the smoothing of climate information; the advantage is that it is based on a simple physical principle and it is not sensitive to local or short-term climate fluctuations.

Two records have been obtained so far for the low-latitude Americas, i.e., for southern Texas (Stute et al., 1992) and northeastern Brazil (Stute et al., 1995). Both records indicate a 5°C cooler climate during the last glacial maximum.

17.4. A BRIEF REVIEW OF PALEOTEMPERATURE SIGNALS FROM SELECTED LOWLAND RECORDS

The first record of glacial age sediment from Central America was from beneath Lake Gatún (ca. −30 m elevation compared with modern sea level) in Panama (Bartlett and Barghoorn, 1973) (Fig. 2). Lake Gatún was formed when the Panama Canal was constructed and the Chagres River was dammed. Marshes that once flanked the Chagres and Trinidad Rivers are now submerged by Lake Gatún. Cores raised from the flooded marshes provided sediments that were riverine in origin. Because of the potential inclusion of pollen that had been reworked or transported long distances, Flenley (1979) urged caution in their interpretation. However, the source rivers drain low-elevation basins that presently would not support montane forest elements.

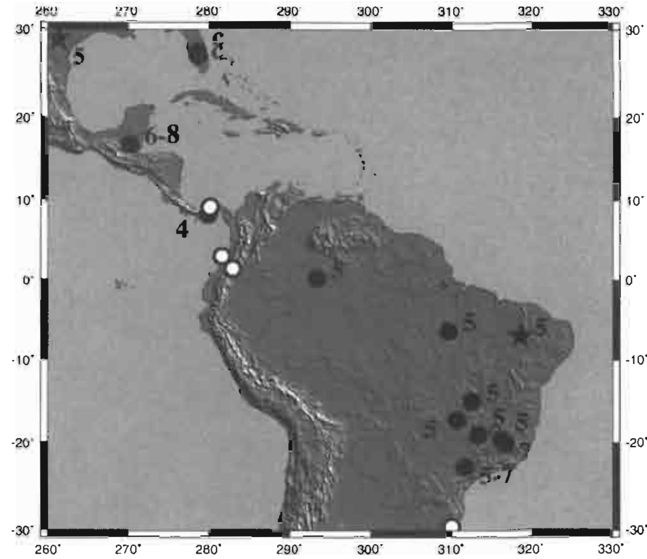

FIGURE 2 Locations and cooling estimates for sites in the lowland neotropics and subtropics at the last glacial maximum. Numbers indicate degrees Celsius (°C) of cooling compared with modern temperatures. Where the cooling is not quantified, it is indicated by "c." Sites marked with a circle are based on pollen records; those marked with a star are based on groundwater isotopic data.

Indeed, the modern pollen rain throughout their catchment areas would be remarkably uniform (Bush, personal observation). The largest changes in pollen abundance in this record reflect the migration of mangrove in response to changes in sea level. However, the presence of *Iriartea*, Ericaceae, *Ilex*, and *Podocarpus* pollen in late glacial assemblages indicates a downslope migration of these taxa of between 500 and 1000 m. Bartlett and Barghoorn suggested that this downslope shift represented a minimum temperature depression of 2.5°C. In an extensive study of modern pollen rain in Panama, Bush et al. (personal observation) did not find *Iriartea* pollen in any assemblage at less than 1000 m. Assuming a lapse rate of 5.5°C / 1000 m, it would appear likely that the Gatún record documents at least a 5°C cooling. The complete lack of *Quercus* pollen in this record is striking, as pollen of this genus is abundant at two central Panamanian sites of glacial age (El Valle, 500 m: Bush and Colinvaux, 1990; and La Yeguada, 650 m: Bush et al., 1992). The modern pollen rain study shows *Quercus* to be ubiquitous above 1700 m elevation, and so we may infer that the temperature depression was not sufficient to bring *Quercus* down to sea level. Thus, the cooling would not have exceeded 8°C.

At Lake Quexil in Guatemala (Leyden et al., 1993, 1994), the coolest time on record was between 24,000 and 14,000 ^{14}C B.P., when temperatures were between 6° and 8°C lower than present values. As there is clear evidence of drying during the glacial maximum at this site, it is possible that there would have been some steepening of the lapse rate. For this reason, Leyden considers the lower of these estimates to be more realistic.

The first compelling evidence that glacial cooling affected the Amazon basin came with the discovery of *Podocarpus* timber at 1100 m elevation at Mera, Ecuador (Liu and Colinvaux, 1985). Equatorial *Podocarpus* species are almost exclusively montane, seldom living at elevations lower than 1800 m. Liu and Colinvaux (1985) inferred a temperature depression of ca. 4°C for the period between 33,000 and 30,000 ^{14}C B.P. on the basis of this evidence. A more detailed analysis of the sediments and the discovery of a second site at San Juan Bosco (970 m elevation) in Ecuador widened the list of cool indicator taxa to include *Magnolia, Drimys, Alnus, Hedyosmum, Weinmannia,* and grasses of the three-carbon (C3) photosynthetic pathway. With further dating, a cooling of 7.5°C was suggested for the period from 33,000–30,000 ^{14}C B.P. and 4°C for the period from 30,000–26,000 ^{14}C B.P. (Bush et al., 1990).

Since 1990, new data sets for different lowland ecosystems have produced further evidence of a substantial temperature depression during the glacial period. Lagoa Crominia in the Cerrado of central Brazil suggested a cooling of 5°C at 18,000 ^{14}C B.P. (Ferraz-Vicentini and Salgado-Labouriau, 1996). Lagoas dos Olhos and Serra Negra (De Oliveira, 1992) and the swamp of Salitre (Ledru, 1993) all document the Pleistocene expansion of *Araucaria* forests. Records for southern Brazil indicate the expansion of subtropical grasslands (Behling and Lichte, 1997; Behling et al., 1998). In each case, a 5°C lowering of temperature during glacial times is inferred. In the lowland Amazon, lakes perched atop massifs, such as the Serra dos Carajas (Absy et al., 1991) and the Hill of Six Lakes (Colinvaux et al., 1996), have provided long records of the lowland forest environment. The Carajas record is interpreted by Absy et al. (1991) primarily in terms of wet and dry events, but the pollen record is consistent with a glacial cooling (Absy, personal communication). Two records from the Hill of Six Lakes contain significant amounts of *Podocarpus, Hedyosmum,* and *Weinmannia* pollen, leading to the suggestion of a 5°C glacial cooling (Colinvaux et al. 1996).

17.5. THE DATA SET TO DATE: 30°N TO 30°S

Table 1 presents a summary of available data documenting paleotemperature at 18,000 ^{14}C B.P. for the tropical and extratropical regions of the New World.

17.6. DISCUSSION

It is evident from this data set that few records have sediments explicitly dated to 18,000 ^{14}C B.P. Ledru (1992) and Ledru et al. (1998) have suggested that the period from ca. 25,000–16,000 ^{14}C B.P. was a time of regionwide aridity in which most lake basins dried out. A priori arguments, such as a cooler ocean and land surface would have reduced evaporation, and hence cloud formation, and weakened circulations would have brought less moisture onshore, are powerful. Some reduction in precipitation and lake levels during the last glacial is very likely. There is no question that depositional rates slowed at a number of sites from Panama to Brazil during this period. However, more sites and better dating are needed before it can be resolved whether this period was a single phase of major widespread aridity or local asynchronous drying events.

With our paucity of sites, the vastness of the area considered, and current inability to assess paleoprecipitation from pollen records (see Colinvaux et al., 2000, for a review, and a contrasting review by Hooghiemstra and van der Hammen, 1998), it is to be expected that there will be considerable debate within our community over the extent and duration of possible dry events. Divergent views are held within this group of authors; however, none espouse such serious drying as to elevate lapse rates sufficiently to explain away the signature of cooling.

17.6.1. The Potential Influence of CO_2 and UV Radiation on Past Vegetation Assemblages

Street-Perrott et al. (1997) suggested that past concentrations of CO_2 may have been at least as important as cooling in determining the elevation at which species grew during glacial times. They suggest that under glacial conditions, with atmospheric concentrations of CO_2 close to 180 ppm, plants using the four-carbon photosynthetic pathway (C4) or crassulacean acid metabolism (CAM) would be expected to outcompete those using the C3 pathway. It has been argued that, in Africa, the lowering of tree lines apparent in some pollen records was, in part, an artifact of palynologists' inability to resolve the difference between C3 (montane) and C4 (lowland) grasses (Street-Perrott et al., 1997). Street-Perrott et al. suggest that instead of an invasion of midelevations by C3 grasses, high Poaceae pollen percentages reflect C4 grasses outcompeting seedlings of C3 trees during the glacial maximum.

The principal problem encountered by a C3 plant faced with low CO_2 concentrations is drought stress (Woodward 1993). In western Amazonia and on the

TABLE 1 Locations, Ages, and Paleotemperature Data for Lowland Neotropical Sites Used in Reconstructions of Paleotemperature at 18,000 ^{14}C B.P.[a]

Site	Latitude, longitude	Elevation (m)	Dates	Lab no.	Calibrated years B.P. min. cal. age (cal. age) max. cal. age	Delta T°C at 18,000 (21,500)	Max. cooling	Date of max. cooling	Ref.
Carrizo Aquifer (U.S.A.)	29°N, 98°40′W	−98.75	10,600 ± 3,000		19,560 (12,530) 5,300	−5	−5	Uniform	Stute et al., 1992
								throughout	Stute and
			11,700 ± 3,000		17,600 (13,640) 9,650			period	Clark,
			20,800 ± 3,000		[24,400]			considered	unpublished
			27,200 ± 3,000		[30,500]				^{14}C data
Lake Annie (U.S.A.)	27°12′N, 81°25′W	40	4,715 ± 95	I-6889	5,580 (5,350) 5,310	Cooler,			Watts, 1975
			13,010 ± 165	I-6888	15,730 (15,450) 15,150	unquan-			
			37,000 ± 3,200	I-6025	[38,900]	tified			
Lake Tulane (U.S.A.)	27°35′N, 81°30′W	34	9,810 ± 90	WIS-1753	11,000 (10,990) 10,950	Cooler,			Grimm et al., 1993
			10,940 ± 120	WIS-1648	12,980 (12,860) 12,740	unquan-			
			13,730 ± 130	WIS-1649	16,650 (16,460) 16,270	tified			
			17,170 ± 210	WIS-1754	20,720 (10,350) 20,000				
			20,380 ± 239	WIS-1650	[24,000]				
			24,240 ± 400	WIS-1755	[27,700]				
			26,120 ± 440	WIS-1651	[29,500]				
			32,300 ± 450	QL-4630	[34,900]				
			35,700 ± 650	QL-4631	[37,800]				
			>33,000	WIS-1652	>[35,500]				
			35,600 ± 400	QL-4057	[37,700]				
			39,600 ± 500	QL-4058	[41,100]				
			>46,000	QL-4632	>[46,600]				
Quexil (Guatemala)	16°55′N, 89°49′W	110	10,750 ± 460	SI-5257	13,120 (12,680) 12,130	−6 to −8	−6.5 to −8	24,000 (27,500) to 14,000 (16,800)	Leyden et al., (1993)
			10,300 ± 110	AA-3062	12,330 (12,150) 11,900				
			10,630 ± 110	AA-3063	12,680 (12,560) 12,420				
			12,790 ± 60	b-92902	15,270 (15,100) 14,910				
			27,450 ± 500	AA-3064	[30,800]				
Lake Gatún (Panama)	9°16′N, 79°52′W	−30	9,600 ± 300	UCLA-185	11,000 (10,750) 10,220	N/A	−2.5	11,000 (12,900) to 10,000 (11,200)	Bartlett and Barghoorn, 1973
			11,300 ± 200	UCLA-186	13,430 (13,210) 13,010		reinter-		
	9°11′N, 79°57′W		35,500 ± 2,500	UCLA-1025	[37,600]		preted as		
							−5		
La Yeguada (Panama)	8°27′N, 80°51′W	650	8,840 ± 130	b-26102	9,970 (9,880) 9,650	N/A	−6	14,000 (16,800) to 12,000 (14,000)	Bush et al., 1992
			10,210 ± 130	b-25923	12,240 (11,980) 11,340				
			10,530 ± 100	b-24739	12,580 (12,450) 12,310				
			11,250 ± 140	b-24738	13,310 (13,160) 13,010				
			11,610 ± 180	b-25924	13,770 (13,160) 13,330				
			14,230 ± 370	b-25925	17,490 (17,060) 16,610				
			13,670 ± 210	b-25696	16,660 (14,430) 13,830				
			12,910 ± 140	b-24241	15,340 (15,290) 15,020				

(continues)

TABLE 1 (*continued*)

Site	Latitude, longitude	Elevation (m)	Dates	Lab no.	Calibrated years B.P. min. cal. age (cal. age) max. cal. age	Delta T°C at 18,000 (21,500)	Max. cooling	Date of max. cooling	Ref.
El Valle (Panama)	8°20′N, 80°10′W	500	8,330 ± 150	b-27721	9,450 (9,370) 9,040	−4	−6	14,000 (16,800)	Bush and Colinvaux, 1990
			14,180 ± 250	b-29038	17,300 (17,000) 16,700				
			19,420 ± 330	b-27722	[23,100]				
			31,850 ± 1,800	b-27723	[34,500]				
			>35,000	b-27724	>[37,200]				
			30,720 ± 800	b-25697	[33,600]				
San Juan Bosco (Ecuador)	3°3′N, 78°27′W	970	26,020 ± 300	b-27144	[29,400]	N/A	−7.5	ca. 33,000 (35,500)	Bush et al., 1990
			30,990 ± 350	b-27145	[33,800]				
Mera (Ecuador)	1°29′N, 77°06′W	1100	26,530 ± 270	b-10170	[29,600]	N/A	−7.5	33,000 (35,500)	Bush et al., 1990
			31,870 ± 970	b-27143	[34,500]				
			33,520 ± 1,010	b-9618	[35,900]				
Lagoa Pata (Brazil)	0°16′N, 66°41′W	250–300	5,800 ± 70	b-63417	6,720 (6,630) 6,490	−5	−5	14,000 (16,800)	Colinvaux et al., 1996
			14,230 ± 60	b-91489	17,170 (17,060) 16,950				
			15,560 ± 60	b-90306	18,570 (18,460) 18,360				
			17,840 ± 300	b-75109	21,700 (21,280) 20,840				
			18,020 ± 70	b-90307	21,700 (21,510) 21,320				
			30,830 ± 220	b-91490	[33,600]				
			31,390 ± 540	b-75110	[34,200]				
			32,010 ± 630	b-88941	[34,700]				
			34,650 ± 420	b-89715	[36,900]				
			37,830 ± 1,300	b-88942	[39,600]				
			38,860 ± 920	b-68529	[40,500]				
			42,010 ± 1,240	b-68530	[43,200]				
Lagoa Verde (Brazil)	0°16′N, 66°41′W	250–300	12,050 ± 50	CAMS-47775	14,190 (14,050) 13,920	−5	−5	?	Bush et al., unpublished
			2,790 ± 50	CAMS-47776	2,940 (2,860) 2,790				
			12,480 ± 60	b-95704	14,800 (14,620) 14,450				
			17,100 ± 70	CAMS-47777	20,480 (20,250) 20,050				
			16,410 ± 70	CAMS-47778	19,470 (19,310) 19,170				
			18,430 ± 100	b-95705	[22,200]				
			19,740 ± 70	b-95706	[23,400]				
			19,170 ± 120	CAMS-47779	[22,900]				
			18,680 ± 130	CAMS-47780	[22,400]				
			23,600 ± 450	OS-1320	[27,100]				
			>43,800	OS-1321	>[44,700]				

Carajas	6°20′S, 50°25′W	700	10,460 ± 150		12,550 (12,370) 12,150	−5	−5	9000 (10,000)	Absy et al.,
(Brazil)			12,520 ± 120		14,920 (14,680) 14,450				1991
			22,870 ± 500		[26,400]				
			23,670 ± 500		[27,200]				
			24,520 ± 820		[28,100]				
			28,660 ± 1,000		[31,800]				
			51,200 ± 2,000		[51,200]				
Serra Grande	7°S, 41°30′W	−41.50	13,100 ± 3,000		18,980 (15,590) 11,680	−5	−5	Uniform	Stute et al.,
Aq (Brazil)			14,800 ± 3,000		21,240 (17,700) 13,750			throughout	1995
			16,000 ± 3,000		22,700 (18,860) 15,300			period	
								considered	
Aguas	15°S, 47°35′W	1040	7,220 ± 50	OBDY 1152	8,060 (7,960) 7,930	−5	−5	14,000 (16,800)	Barberi et al.,
Emendadas			21,450 ± 100	OBDY 1193	[25,100]				1995
Crominia	17°17′S, 49°25′W	710	6,680 ± 90	UtC 45715	7,560 (7,490) 7,400	−5	−5	14,000 (16,800)	Ferraz-
(Brazil)			13,150 ± 50	OBDY 956	15,800 (15,670) 15,530				Vicentini and
			32,060 ± 520	UtC 45716	[34,700]				Salgado-
			32,390 ± 680	UtC 64283	[35,000]				Labouriau,
			32,580 ± 1,640	UtC 45717	[35,100]				1996
Lagoa dos	19°38′S, 43°54′W	730	6,710 ± 140	b-53327	7,640 (7,540) 7,400	−5			De Oliveira,
Olhos (Brazil)			15,530 ± 110	b-53328	18,570 (18,440) 18,300				1992
			19,410 ± 160	b-35394	[23,100]				
Serra Negra	19′S, 46°45′W	1170	14,280 ± 90	b-53314	17,250 (17,120) 16,990	−5	−5		De Oliveira,
(Brazil)			39,930 ± 540	b-53315	[41,400]				1992
			>46,180	b-53321	>[46,800]				
Salitre	19°S, 46°46′W	1050	9,150 ± 80	OBDY 570	10,280 (10,040) 10,010	−5	−5	11,000 (12,900)	Ledru, 1993
(Brazil)			10,440 ± 110	OBDY 495	12,490 (12,350) 12,170				
			10,350 ± 230	OBDY 496	12,520 (12,230) 11,720				
			12,890 ± 80	OBDY 550	15,440 (15,260) 15,060				
			14,230 ± 150	OBDY 571	17,250 (17,060) 16,870				
			16,800 ± 100	OBDY 552	20,050 (19,820) 19,610				
			28,740 ± 500	OBDY 470	[31,900]				
			32,030 ± 500	OBDY 471	[34,700]				
			>50,000		>[50,000]				
Catas Altas	20°05′S, 43°22′W	755	8,310 ± 295	Hv20825	9,520 (9,300) 8,780	−7	−7	28,000 (31,300) to	Behling, 1998
(Brazil)			20,490 ± 165	Hv20826	[24,100]			18,000 (21,500)	
			19,960 ± 530	Hv20827	[23,600]				
			21,550 ± 440	Hv20828	[25,200]				
			22,087 ± 1,580/ −2,190	Hv20829	[25,700]				
			37,880 ± 930	Hv20830	[39,700]				
			>47,740	Hv20831	>[48,100]				
Botucatu	22°48′S, 48°23′W	770	5,678 ± 37	UtC-5544	6,490 (6,450) 6,410	−5 to −7	−5 to −7		Behling et al.,
(Brazil)			19,180 ± 190	Hv-20824	[22,900]				1998
			25,750 ± 170	UtC-5545	[29,200]				
			22,900 ± 130	UtC-5546	[26,400]				
			>32,360	Hv-20824	>[34,900]				

[a]Calendar ages were calculated with CALIB 3.0.3c (Stuiver and Reimer, 1993) for the interval up to 18,367 ^{14}C.B.P. In the interval from 18,367 to 27,120 ^{14}C B.P., a linear conversion is used assuming corresponding calendar ages of 22,115 and 27,120 cal. years B.P., respectively. The calendar ages are based on Bard et al. (1990). For the interval 27,120–50,000 ^{14}C B.P., Mommersteeg (1998) assumes a difference of 3350 cal. years at 27,120 ^{14}C B.P., which gradually diminished to a difference of zero calendar years at an age of 50,000 ^{14}C B.P., based on the work of Mazuad et al. (1991) and Laj et al. (1996). Calibrated ages are shown in parentheses, flanked by a 1 sigma age range.

Andean flanks, where rainfall can exceed 5 m/year, drought is less of a problem than for plants on the slopes of Mt. Kenya. Generally, in the neotropics the plants that are observed invading new areas during glacial times are C3 trees. Indeed, where Poaceae did become more abundant at San Juan Bosco and Mera, it was determined on the basis of their phytoliths that C3 grasses were invading areas presently occupied by C4 grasses (Bush et al., 1990). The replacement of C4 with C3 grasses clearly runs counter to the pattern expected if CO_2 were the factor most limiting to plant growth. Cooling rather than low CO_2 concentrations is a more likely cause of this invasion.

At drier locations, such as the Carajas plateau, which receives ca. 2000 mm of precipitation per annum, or across much of the eastern flank of Amazonia, it is possible that reduced precipitation during glacial periods could have provided C4 and CAM plants with a competitive advantage. Indeed, at Carajas, the facultative CAM plant *Cuphea* increases in abundance during glacial times (Absy et al., 1991). However, plenty of C3 trees remain in the glacial landscape, and the greatest peaks of grasses (potentially a major C4 component of vegetation) occur in the Holocene, not during the Pleistocene. Overall, low concentrations of CO_2 cannot be discounted as an important ecological factor in these drier parts of the neotropics, but they do not appear to be as important as temperature effects.

Reduced CO_2 concentrations and reduced cloud cover could result in increased inputs of ultraviolet (UV) radiation at the Earth's surface (Flenley, 1993). Flenley (1998) suggested that under these circumstances montane plants that are more highly adapted to UV radiation would have a competitive advantage. The highest elevations would have had the most exposure to UV radiation and would have experienced the greatest change in incoming radiation. Flenley suggests that some of the difference observed in paleotemperature between the highest and lowest locations may be attributable to changes in UV radiation. In the Andes, the differential in cooling between 2550 m elevation and the lowland elevations appears to have been ca. 3°C at 18,000 ^{14}C B.P., reflecting a cooling of 8°C for the Sabana de Bogotá and ca. 5°C at sites below 1000 m elevation. Although some part of this temperature discrepancy between high- and lower elevation sites might be attributable to the effects of UV radiation, a larger variable is likely to be the error of the methods used to estimate paleotemperature.

17.6.2. The Timing of Peak Cooling

From our data set, even though there are 16 records from the lowland neotropics and subtropics that span the period of 18,000 ^{14}C B.P., only half have sediments directly dated to between 16,000 and 20,000 ^{14}C B.P. The available records document a 5°C cooling for this period, which is typical of late Pleistocene times; i.e., it was not especially cold. Several, though certainly not all, records show pronounced cold events at approximately 33,000–30,000 ^{14}C B.P., when temperatures may have dipped as much as 7.5°C below present levels, and again at ca. 14,000 ^{14}C B.P., with temperatures between 5° and 6°C cooler than present levels. These episodes of more intense cooling appear to coincide with phases of glacial re-advance in Ecuador (Clapperton, 1987; Seltzer, 1990), whereas no distinct re-advance at 18,000 ^{14}C B.P. has been documented for any of the tropical Andean glaciers. However, the cooling evident in the records of San Juan Bosco and Mera at 33,000–30,000 ^{14}C B.P. does not appear to have been influenced by precipitation, and at least two data points suggest this time to have been both wet and very cold (Bush et al., 1990). While the terrestrial pollen data provide no regional consensus for the timing of maximal cooling, they suggest that the period from 33,000–12,000 ^{14}C B.P. was predominantly cold with marked local climatic events that provided oscillations between warmer and cooler conditions. This is supported by a continuous pollen record from the Amazon deep-sea fan, spanning the last 50,000 years B.P., which shows a maximum contribution from cold-adapted taxa, such as *Podocarpus* and *Hedyosmum*, between 19,800 and 11,000 cal. B.P. (Haberle and Maslin, 1999).

It is also important to note that the terrestrial paleoclimatic records for other tropical regions are in close accord with our estimate for the neotropics. In Southeast Asia, lower montane rain forest taxa invaded the bottomland rain forest, and Flenley (1998) suggests a mean annual temperature depression of 6°–10°C (Flenley, 1998). In Africa, numerous high-elevation pollen records documented a descent of forest that would have required a cooling of ca. 9°C (e.g., Coetzee, 1964; Livingstone, 1967; Taylor, 1990); but in the lowlands, the cooling appears to have been more modest (Giresse et al., 1994). In a study of African lowland sites using transfer functions derived from a suite of modern analogs, Bonnefille et al. (1990) estimated a cooling of 4° ± 2°C. Street-Perrott et al. (1997) suggest that when CO_2 effects are factored in, even at high elevations, the actual cooling may have been closer to 2°C.

Just as some tropical cooling is a consistent pattern, the extent of precipitation change is variable. Indeed, none of the tropical regions show a consistent pattern, and the pattern seen in Amazonia of some sites appearing to dry while others remained humid is repeated in Africa and Southeast Asia (see Flenley, 1998 for a summary).

17.6.3. Implications of Cooled Tropical Lowlands

The descent of upland vegetation elements 1000 m below their modern limits is apparent in both high- and low-elevation pollen records at 18,000 ^{14}C B.P. As humid conditions extended from the foot of the Andes to 2500 m elevation, it is safe to assume a lapse rate that approximated to 5°C / 1000 m of ascent, and thereby a 5°C cooling. Another way to view this is that frost may have occurred as low as 800 m elevation at the equator. Other critical temperature thresholds, such as permanent damage to plant lipid membranes that occurs between 8 and 13°C (Graham and Patterson, 1982), are likely to have been experienced in all but the most sheltered locations. Cold stress would have affected populations throughout the study area, causing the reassortment of species into unique communities. Populations at the tips of peninsulas such as Florida, on islands, and close to the equator could not have migrated to escape cold episodes and may have experienced the greatest species losses. Given that this last glacial interval was not significantly colder than those that had preceded it in the Quaternary, a wave of extinctions would not be expected. Any truly cold-intolerant species would have been eliminated by earlier glacial episodes, possibly explaining the greater diversity of Miocene than Holocene palynomorphs in Amazonia (van der Hammen and Absy, 1994). However, as in the midlatitudes, from Florida to the equator and south to the Mato Grosso, the Pleistocene landscape would have been filled with assemblages of plants and animals without modern analogs.

It is apparent that a reconciliation is needed between the marine and terrestrial records. Reconstructions of SSTs suggested that the tropical oceans adjacent to South America had barely cooled at 18,000 ^{14}C B.P. (CLIMAP Project Members, 1981). Temperature depressions of only 1°–2°C were suggested by analysis of foraminiferal communities recovered from deep ocean cores. These reconstructions were based on the comparison of modern analog and fossil communities. At high and midlatitudes, the degree of communality (overlap of modern and fossil assemblages) was strong (approaching 100%), giving confidence to the temperature reconstructions. However, seven of nine cores within 2° latitude of the equator had statistically insignificant communality during the period 20,000–14,000 ^{14}C B.P. (sensu Mix et al., 1986). Weak communality translated to tenuous paleoclimatic reconstructions, yet the CLIMAP (1981) tropical paleotemperatures for 18,000 ^{14}C B.P. were widely accepted. A reevaluation of the CLIMAP data is being conducted (Alan Mix, personal communication), and these results will be eagerly awaited by the terrestrial community. In the meantime, isotopic analyses of Pleistocene Caribbean coral reefs suggest that in these nearshore environments, SSTs were 5°C cooler than present values (Guilderson et al., 1994). A similar cooling of the sea surface was documented by using the relative abundance of double bonds in alkenones from marine sediments (Bard et al., 1997). These investigators inferred a 4°C cooling for the equatorial Atlantic at the time of the last glacial maximum and a cooling of as much as 7°C in some nearshore samples from the Caribbean.

Taking a different approach, Webb et al. (1997) maintained a modern ocean heat transport in their model of glacial SST. After allowing for reduced sea levels, lowered CO_2 concentrations, enlarged ice masses, and energy being channeled through glacial North Atlantic Intermediate Water rather than via the North Atlantic Deep Water, they predicted a 5.5°C cooling of tropical SSTs.

17.7. CONCLUSIONS

Overall, the paleoecologic and isotopic data set from the lowland neotropics reveals a remarkable constancy in the estimate of temperature for the period around 18,000 ^{14}C B.P. In almost all cases, a cooling approximating to 5°C is recorded. It is heartening to find a growing body of independent temperature estimates emerging from the marine and modeling communities that are in close accord with the terrestrial estimates of paleotemperature. The terrestrial data also strongly suggest that brief climatic oscillations lasting a few millennia centered on 30,000 and 14,000 ^{14}C B.P. may have produced even stronger local cooling episodes with temperatures as much as 7.5°C below present levels. Although our community is generally united in its estimate of a lowland neotropical cooling of 5°C for much of the last glacial period, it must be recognized that this is a very crude estimate. We have very few records from an enormous area, and, in many cases, the sedimentary sequences apparently contain gaps or at least rapid changes in depositional rate.

Our community is divided over the important issue of the magnitude and timing of precipitation change during glacial episodes. The forthcoming debate promises to be both vigorous and rewarding, stimulating, it is hoped, the invention of a technique to provide reliable estimates of paleoprecipitation. The only certainty that we have now is that we have too few data to address the issue in any authoritative way.

Although the potential impact of lowered concentrations of CO_2 on the success of individual species is recognized, there is no evidence to suggest that C4 or

CAM plants outcompeted C3 plants in the lowland neotropics. Indeed, the species replacements are almost always one C3 tree replacing another. The influence of changes in CO_2 concentration in this ecosystem is considered to be far smaller than influences of temperature, precipitation, and hydrology. Similarly, while the high elevations of the Andes may have been affected by higher levels of UV radiation during glacial episodes, it seems unlikely that the migration of midelevation or lowland taxa would have been significantly affected.

To unravel the complexities of episodic climatic events within the last glacial cycle, more long records, analyzed in great detail and with good isotopic dating, are clearly needed. In our quest to determine the climatic history of the lowland neotropics, our community has arrived at the starting line, not at the winner's post.

References

Absy, M. L., and T. van der Hammen, 1976: Some palaeoecological data from Rondônia, southern part of the Amazon basin. *Acta Amazonica*, **6**: 293–299.

Absy, M. L., A. Cleef, M. Fournier, L. Martin, M. Servant, A. Sifeddine, M. Ferreira da Silva, F. Soubiès, K. Suguio, B. Turcq, and T. van der Hammen, 1991: Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de L'Amazonie au cours des 60,000 dernières années. Première comparaison avec d'autres regions tropicales. *Comptes Rendus de l' Academie Science Paris, Series II*, **312**: 673–678.

Andrews, J. N., and D. J. Lee, 1979: Inert gases in groundwater from the Bunter Sandstone of England as indicators of age and paleoclimate trends. *Journal of Hydrology*, **41**: 233–252.

Barberi, M., M.-L. Salgado-Labouriau, K. Suguio, L. Martin, B. Turcq, and J.-M. Flexor, 1995: Analise palinologica da vereda de Aguas Emendadas (DF). *V. Congreso da Associacao Brasileira de Estudos do Quaternario*, Universidad Fedderale Fluminense, Niteroi, Rio de Janeiro, Brazil.

Bard, E., B. Hamelin, R. G. Fairbanks, and A. Zindler, 1990: Calibration of the ^{14}C timescale over the past 30,000 years using mass spectrometric U-Th ages from Barbados. *Nature*, **345**: 405–410.

Bard, E., F. Rostek, and C. Sonzogni, 1997: Interhemispheric synchrony of the last deglaciation inferred from alkenone paleothermometry. *Nature*, **385**: 707–710.

Bartlett, A. S., and E. S. Barghoorn, 1973: Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate and sea-level change). *In* Graham, A. (ed.), *Vegetation and Vegetational History of Northern Latin America*. Amsterdam: Elsevier, pp. 203–299.

Behling, H., 1998: Late Quaternary vegetational and climatic changes in Brazil. *Review of Palaeobotany and Palynology*, **99**: 143–156.

Behling, H., and M. Lichte, 1997: Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. *Quaternary Research*, **48**: 348–358.

Behling, H., M. Lichte, and A. W. Miklos, 1998: Evidence of a forest free landscape under dry and cold climatic conditions during the last glacial maximum in the Botucatú region (São Paulo State), Southeast Brazil. *Quaternary of South America and Antarctic Peninsula*, **11**: 99–110.

Bonnefille, R., J. C. Roeland, and J. Guiot, 1990: Temperature and rainfall estimates for the past 40 000 years in equatorial Africa. *Nature*, **346**: 347–349.

Bradbury, J. P., B. W. Leyden, M. Salgado-Labouriau, W. M. Lewis, Jr., C. Schubert, M. Binford, D. G. Frey, D. R. Whitehead, and F. H. Weibezahn, 1981: Late Quaternary environmental history of Lake Valencia, Venezuela. *Science*, **214**: 1299–1305.

Broecker, W. S., 1986: Oxygen isotope constraints on surface ocean temperatures. *Quaternary Research*, **26**: 121–134.

Bush, M. B., and P. A. Colinvaux, 1990: A long climatic and vegetation record from lowland Panama. *Journal of Vegetation Science*, **1**: 105–118.

Bush, M. B., P. A. Colinvaux, M. C. Wiemann, D. R. Piperno, and K.-B. Liu, 1990: Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Research*, **34**: 330–345.

Bush, M. B., D. R. Piperno, P. A. Colinvaux, P. E. De Oliveira, L. A. Krissek, M. C. Miller, and W. E. Rowe, 1992: A 14,300 year paleoecological profile of a lowland tropical lake in Panama. *Ecological Monographs*, **62**: 251–275.

Centro Ecuatoriano de Investigación Geográfica (CEDIG), 1983: *Los Climas Del Ecuador. Documentos de Investigación*, No. 4, Quito, Ecuador.

Clapperton, C. M., 1987: Maximal extent of the late Wisconsin glaciation in the Ecuadorian Andes. *Quaternary of South America and Antarctic Peninsula* **5**: 165–180.

CLIMAP Project Members, 1976: The surface of the ice-age Earth. *Science*, **191**: 1131–1137.

CLIMAP Project Members, 1981: Seasonal reconstruction of the Earth's surface at the last glacial maximum. *Geological Society of America Map and Chart Series*, **36**.

Coetzee, J. A., 1964: Evidence for a considerable depression of vegetation belts during the upper Pleistocene on the east African mountains. *Nature*, **204**: 564–566.

Colinvaux, P. A., P. E. De Oliveira, and M. B. Bush, 2000: Amazonian and neotropical plant communities on glacial time-scales. *Quaternary Science Reviews*, **19**: 141–169.

Colinvaux, P. A., P. E. De Oliveira, E. Moreno, M. C. Miller, and M. B. Bush, 1996: A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science*, **274**: 85–88.

Davis, M. B., 1981: Quaternary history and the stability of forest communities. *In* West, D. C., H. H. Shugart, and D. B. Botkin (eds.), *Forest Succession: Concepts and Application*. New York: Springer-Verlag, pp. 132–154.

De Oliveira, P. E., 1992: A palynological record of late Quaternary vegetational and climatic change in southeastern Brazil. Ph.D. thesis. The Ohio State University, Columbus.

Faegri, K., 1966: Some problems of representativity in pollen analysis. *Palaeobotanist*, **15**: 135–140.

Faegri, K., and J. Iversen, 1989: *Textbook of Pollen Analysis*, 4th ed. Copenhagen: Munksgaard, 328 pp.

Ferraz-Vicentini, K. R., and M. L. Salgado-Labouriau, 1996: Palynological analysis of a palm swamp in central Brazil. *Journal of South American Earth Science*, **9**: 207–219.

Flenley, J. R., 1979: *A Geological History of Tropical Rainforest*. London: Butterworth.

Flenley, J. R., 1993: Cloud forest: The Massenerhebung effect and ultraviolet insolation. *In* Hamilton, L. S., J. O. Juvik, and F. M. Scatena (eds.), *Tropical Montane Cloud Forest: Proceedings of an International Symposium*. East-West Center, Honolulu, pp. 94–96.

Flenley, J. R., 1998: Tropical forests under the climates of the last 30,000 years. *Climatic Change*, **39**: 177–197.

Giresse, P., J. Maley, and P. Brenac, 1994: Late Quaternary paleoenvironments in the Lake Barombi-Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **107**: 65–78.

Graham, D., and B. D. Patterson, 1982: Responses of plants to low, nonfreezing temperatures: Proteins, metabolism and acclimation. *Annual Review of Plant Physiology*, **33**: 347–372.

Grimm, E. C., G. L. Jacobson, Jr., W. A. Watts, B. C. S. Hansen, and K. A. Maasch, 1993: A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich events. *Science*, **261**: 198–200.

Guilderson, T. P., R. G. Fairbanks, and J. L. Rubenstone, 1994: Tropical temperature variations since 20,000 years ago: Modulating interhemispheric climate change. *Science*, **263**: 663–665.

Haberle, S. G., 1998: Late Quaternary vegetation change in the Tari basin, Papua New Guinea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **137**: 1–24.

Haberle, S. G., and M. Maslin, 1999: Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon fan: ODP Site 932. *Quaternary Research*, **51**: 157–183.

Haffer, J., 1969: Speciation in Amazonian forest birds. *Science*, **165**: 131–137.

Haffer, J., 1991: Avian species richness in tropical South America. *Studies in Neotropical Fauna and Environment*, **25**: 157–183.

Hansen, B. C. S., H. E. Wright, and J. P. Bradbury, 1984: Pollen studies in the Junín area, central Peruvian Andes. *Geological Society of America Bulletin*, **95**: 1454–1465.

Heusser, L. E., 1995: Pollen stratigraphy and paleoecologic interpretation of the 160-K.Y. record from Santa Barbara basin, Hole 893A. *In* Kennett, J. P., J. G. Badaulf, and M. Lyle (eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 146. Ocean Drilling Program, College Station, TX, pp. 265–279.

Hooghiemstra, H., 1984: *Vegetational and Climatic History of the High Plain of Bogotá, Colombia: A Continuous Record of the Last 3.5 Million Years. Dissertationes Botanicae*, **79**: 1–368.

Hooghiemstra, H., 1989: Quaternary and upper-Pliocene glaciations and forest development in the tropical Andes: Evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **72**: 11–26.

Hooghiemstra, H., and T. van der Hammen, 1998: Neogene and Quaternary development of the neotropical rain forest: The refugia hypothesis, and a literature review. *Earth Science Reviews*, **44**: 147–183.

Imbrie, J., and N. G. Kipp, 1971: A new micropaleontological method for quantitative paleoclimatology: Application to a late Pleistocene Caribbean core. *In* Turekian, K. K. (ed.), *Late Cenozoic Glacial Ages*. New Haven, CT: Yale University Press, pp. 71–181.

Kutzbach, J. E., and P. J. Guetter, 1986: The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18,000 yrs. *Journal of Atmospheric Sciences*, **43**: 1726–1759.

Laj, C., A. Mazuad, and J.-C. Duplessy, 1996: Geomagnetic intensity and ^{14}C abundance in the atmosphere and ocean during the past 50 kyr. *Geophysical Research Letters*, **23**: 2045.

Ledru, M.-P., 1991: Etude de la pluie pollinique actuelle des forêts du Brésil central: climat, végétation, application à l'étude de l'évolution paléoclimatique des 30 000 dernières années." Unpublished Ph.D. thesis. Museum National d'Histoire Naturelle, Paris, 169 pp.

Ledru, M.-P., 1992: Modification de la végétation du Brásil central entre la dernière époque glaciaire et l'interglaciaire actuel. *Comptes Rendus de l'Academie des Sciences*, Paris, II, **314**: 117–123.

Ledru, M.-P., 1993: Late Quaternary environmental and climatic changes in central Brazil. *Quaternary Research*, **39**: 90–98.

Ledru, M.-P., J. Bertaux, A. Sifeddine, and K. Suguio, 1998: Absence of last glacial maximum records in lowland tropical forest. *Quaternary Research*, **49**: 233–237.

Leyden, B. W., M. Brenner, D. A. Hodell, and J. A. Curtis, 1993: Late Pleistocene climate in the Central American lowlands. *In* Swart, P. K., K. C. Lohmann, J. McKenzie, and S. Savin (eds.), *Climate Change in Continental Records*. Washington, DC: American Geophysical Union, pp. 165–178.

Leyden, B. W., M. Brenner, D. A. Hodell, and J. A. Curtis, 1994: Orbital and internal forcing of climate on the Yucatán Peninsula for the past ca. 36 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **109**: 193–210.

Liu, K.-B., and P. A. Colinvaux, 1985: Forest changes in the Amazon basin during the last glacial maximum. *Nature*, **318**: 556–557.

Livingstone, D. A., 1967: Postglacial vegetation of the Ruwenzori Mountains in equatorial Africa. *Ecological Monographs*, **37**: 25–52.

Marchant R., H. Behling, A. Cleef, S. Harrison, H. Hooghiemstra, V. Markgraf, C. Prentice, M. L. Absy, T. Ager, R. Anderson, C. Baied, S. Bjorck, R. Byrne, M. Bush, J. Duivenvoorden, J. Flenley, P. De Oliveira, B. van Geel, K. Graf, S. Haberle, T. van der Hammen, B. Hansen, S. Horn, P. Kuhry, M.-P. Ledru, B. Leyden, S. Garcia-Lozano, A. B. M. Melief, P. Moreno, N. T. Moar, A. R. Prieto, G. van Reenen, M. L. Salgado-Labouriau, F. Schabitz, and E. J. Schreve-Brinkman, in press: Pollen-based biome reconstructions for Latin America at 0, 6000 and 18,000 radiocarbon years. *Journal of Biogeography BIOME 6000 Special Issue*.

Markgraf, V., 1993: Climatic history of Central and South America since 18,000 yr ^{14}C B.P.: Comparison of pollen records and model simulations. *In* Wright, H. E., Jr., J. E. Kutzbach, T. Webb, III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein (eds.), *Global Climates Since the Last Glacial Maximum*. Minneapolis: University of Minnesota Press, pp. 357–386.

Martin, P. S., 1964: Paleoclimatology and a tropical pollen profile. Report of the VIth International Congress on the Quaternary, Warsaw, 1961, Vol. ii, pp. 319–323. Paleoclimatological section, Lodz. (Also Contribution 46, Program in Geochronology, University of Arizona, Tucson.)

Mazor, E., 1972: Paleotemperatures and other hydrological parameters deduced from noble gases dissolved in groundwaters, Jordan Rift Valley, Israel. *Geochimica Cosmochimica Acta*, **36**: 1321–1336.

Mazuad, A., C. Laj, E. Bard, M. Arnold, and E. Tric, 1991: Geomagnetic field control of ^{14}C production over the last 80 kyr: Implications for the radiocarbon time-scale. *Geophysical Research Letters*, **18**: 1885–1888.

Mercer, J. H., and O. Palacios, 1977: Radiocarbon dating of the last glaciation in Peru. *Geology*, **5**: 600–604.

Mix, A. C., W. F. Ruddiman, and A. McIntyre, 1986: Late Quaternary paleoceanography of the tropical Atlantic. 1. Spatial variability of annual mean sea-surface temperatures, 0–20,000 years ^{14}C B.P. *Paleoceanography*, **1**: 43–66.

Mommersteeg, H., 1998: Vegetation development and cyclic and abrupt climatic changes during the late Quaternary: Palynological evidence from the Colombian Eastern Cordillera. Ph.D. thesis. Hugo de Vries Laboratory, University of Amsterdam.

Rind, D., and D. Peteet, 1985: Terrestrial conditions at the last glacial maximum and CLIMAP sea-surface temperature estimates: Are they consistent? *Quaternary Research*, **24**: 1–22.

Seltzer, G. O., 1990: Recent glacial history and paleoclimate of the Peruvian-Bolivian Andes. *Quaternary Science Reviews*, **9**: 137–152.

Smith, F. A., and J. L. Betancourt, 1998: Response of bushy-tailed woodrats (*Neotoma cinerea*) to late Quaternary climatic change in the Colorado Plateau. *Quaternary Research*, **50**: 1–11.

Street-Perrott, A. F., Y. Huang, R. A. Perrott, G. Eglinton, P. Barker, L. B. Khelifa, D. D. Harkness, and D. O. Olago, 1997: Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science*, **278**: 1422–1426.

Stuiver, M., and P. J. Reimer, 1993: Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon*, **35**: 215–230.

Stute, M., and P. Schlosser, 1993: Principles and applications of the noble gas paleothermometer. *In* Swart, P. K., K. C. Lohmann, J. McKenzie, and S. Savin (eds.), Climate Change in Continental

Isotopic Records. Washington, DC: American Geophysical Union, *Geophysical Monograph* **78**: 89–100.

Stute, M., M. Forster, H. Frischkorn, A. Serejo, J. F. Clark, P. Schlosser, W. S. Broecker, and G. Bonani, 1995: Cooling of tropical Brazil (5°C) during the last glacial maximum. *Science*, **269**: 379–383.

Stute, M., P. Schlosser, J. F. Clark, and W. S. Broecker, 1992: Paleotemperatures in the southwestern United States derived from noble gas measurements in groundwater. *Science*, **256**: 1000–1003.

Taylor, D. M., 1990: Late Quaternary pollen records from two Ugandan mires: Evidence for environmental change in the Rukiga highlands of southwest Uganda. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **80**: 283–300.

van der Hammen, T., 1963: A palynological study on the Quaternary of British Guiana. *Leidse Geologische Mededelingen*, **29**: 125–180.

van der Hammen, T., 1974: The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, **1**: 3–26.

van der Hammen, T., and M. L. Absy, 1994: Amazonia during the last glacial. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **109**: 247–261.

van der Hammen, T., and E. Gonzalez, 1960: Upper Pleistocene and Holocene climate and vegetation of the Sabana de Bogotá (Colombia, South America). *Leidse Geologische Mededelingen*, **25**: 126–315.

van der Hammen, T., and H. Hooghiemstra, 2000: Neogene and Quaternary history of vegetation, climate and plant diversity in Amazonia. *Quaternary Science Reviews*, **19**: 725–742.

Vanzolini, P. E., 1970: Zoologia sistematica, geografia e a origem das especies. *Instituto Geografico São Paulo. Serie Teses e Monografias*, **3**: 1–56.

Watts, W. A., 1975. A late Quaternary record of vegetation from Lake Annie, south-central Florida. *Geology*, **3**: 344–346.

Webb, R. S., D. H. Rind, S. J. Lehmann, R. J. Healy, and D. Sigman, 1997: Influence of ocean heat transport on the climate of the last glacial maximum. *Nature*, **385**: 695–699.

Webb, T., III, 1987: The appearance and disappearance of major vegetational assemblages: Long term vegetational dynamics in eastern North America. *Vegetatio*, **69**: 177–188.

Webster, P., and N. Streten, 1978: Late Quaternary ice-age climates of tropical Australasia, interpretation and reconstruction. *Quaternary Research*, **10**: 279–309.

Wijmstra, T. A., 1969: Palynology of the Alliance well. *Geologie en Mijnbouw*, **48**: 125–133.

Woodward, F. I., 1993: Plant responses to past concentrations of CO_2. *Vegetatio*, **104/105**: 145–155.

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